

EFFECT OF LEAF ROLLING ON GAS EXCHANGE AND LEAF TEMPERATURE OF ANDROPOGON GERARDII AND SPARTINA PECTINATA

SCOTT A. HECKATHORN AND EVAN H. DeLUCIA

Department of Plant Biology, University of Illinois, Urbana, Illinois 61801

We examined the effect of leaf rolling on CO₂ and water vapor exchange of two C₄ prairie grasses with contrasting patterns of leaf rolling. *Andropogon gerardii* (big bluestem) is a drought-resistant species with predominantly hypostomatal leaves that fold (adaxial surface inward) in response to low leaf water potential, while leaves of *Spartina pectinata* (prairie cordgrass), a mesic species, are epistomatal and roll into spirals (also adaxial surface inward). Adaxial stomata of both species are closed in completely rolled or folded leaves; thus these leaf movements have a minor effect on total leaf conductance. Energy budget calculations indicate that leaf rolling reduces transpiration by 7%–13% in water-stressed plants by lowering leaf temperature and, therefore, leaf-to-air vapor pressure deficit. This reduction is small relative to the direct effect of stomatal closure on transpiration. However, small decreases in transpiration, leaf temperature, and incident irradiance associated with leaf rolling may decrease the potential for photoinhibition, prolong physiological activity, and increase survival during drought.

Introduction

Leaf movements are common adaptive responses to water stress in plants and are important in reducing incident irradiation, leaf temperature, and transpiration (BEGG 1980; EHLERINGER and FORSETH 1980). Such responses include the heliotropic leaf movement observed in many desert species (EHLERINGER and FORSETH 1980; FORSETH and EHLERINGER 1983) and leaf rolling in grasses (REDMANN 1985). Leaf rolling decreases transpiration through changes in leaf conductance and “effective” (displayed or projected) leaf area (BEGG 1980), though it has been argued that the most important effect of leaf rolling is reduction of leaf temperature via decreases in incident irradiation (RIPLEY and REDMANN 1976). The effect of leaf rolling on transpiration (E) may vary among species and is dependent on stomatal distribution and the degree and pattern of stomatal opening in rolled leaves.

REDMANN (1985) presented a conceptual model describing stomatal behavior as leaves roll; however, empirical studies of the effect of leaf rolling on gas exchange have been rare. OPPENHEIMER (1960) reported large decreases in E due to leaf rolling in Mediterranean and Saharan grasses. O'TOOLE and CRUZ (1979) observed a decrease in E in artificially rolled well-watered rice leaves, and the effect of rolling became more pronounced as wind speed increased. They suggested that leaf rolling may augment stomatal closure in reducing water loss. Most studies of water-stress effects on gas exchange in grasses have disregarded changes in effective leaf area and

boundary layer thickness following rolling when calculating fluxes of water vapor and CO₂ (e.g., REDMANN 1971; BROWN and TRILICA 1977; KEMP and WILLIAMS 1980; BARNES 1985; KNAPP 1985). Furthermore, the effect of rolling on total leaf conductance to water vapor in drought-stressed plants has not been examined, and the common assumption that rolling functions to reduce water loss during drought has not been demonstrated experimentally.

The purpose of this study was to determine how leaf rolling affects gas exchange in water-stressed *Andropogon gerardii* Vitman (big bluestem) and *Spartina pectinata* Link (prairie cordgrass). These species are common C₄ grasses native to tallgrass prairie but have contrasting patterns of leaf rolling.

Material and methods

Seeds of *Andropogon gerardii* Vitman and *Spartina pectinata* Link from the Konza Prairie Research Natural Area (Manhattan, Kans.) were germinated in 15-cm plastic pots containing soil, peat moss, calcite clay, and perlite (2:1.5:1:1, v/v). *Andropogon gerardii*, the dominant grass in most tallgrass prairies (WEAVER and FITZPATRICK 1932), is relatively drought-resistant (KNAPP 1985) and has predominantly hypostomatal leaves (KNAPP and GILLIAM 1985) that fold in response to water stress (fig. 1). *Spartina pectinata*, a mesic species primarily restricted to moist swales (WEAVER and FITZPATRICK 1932), is epistomatal, with stomates located in deep longitudinal furrows on the adaxial surface of the leaf (personal observation). Leaves of *S. pectinata* roll into tight spirals in response to water stress (fig. 1).

Following germination, plants were thinned to one per pot and grown in a glasshouse under ca. 28 C day and 20 C night. Supplemental lighting from multivapor HID lamps was used to increase irradiance and extend the photoperiod to 14 h.

Manuscript received September 1990; revised manuscript received April 1991.

Address for correspondence and reprints: S. A. HECKATHORN, Department of Plant Biology, University of Illinois, 289 Morrill Hall, 505 South Goodwin Avenue, Urbana, Illinois 61801.

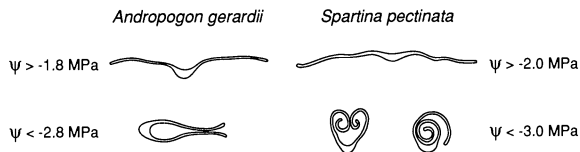


FIG. 1.—Illustrations of transverse sections of open and rolled leaves of *Andropogon gerardii* (left) and *Spartina pectinata* (right). Open leaf width is 1.0 cm for *A. gerardii* and 1.5 cm for *S. pectinata*. Leaves are shown in their natural orientation.

Maximum irradiance at pot height ranged from 700 to 1,800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PPFD). Plants were watered daily and fertilized biweekly with either a commercial NPK (12:31:14) fertilizer or a complete nutrient solution (EPSTEIN 1972).

After 9 wk, plants were transferred to a growth chamber where temperature and photoperiod were maintained as above. Relative humidity was 50% and irradiance at canopy height was 500–600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Two weeks later a drought was initiated by decreasing daily watering to an amount sufficient only to moisten the soil surface. Water was not completely withheld, to ensure a gradual drought.

Net carbon assimilation (A) and E were measured daily throughout the drought using a portable, open-flow, infrared gas-analysis system (model LCA-2, Analytical Development Co., England). The CO_2 concentration of air entering the leaf cuvette was maintained at 350–360 cm^3/m^3 by mixing compressed air and 1% CO_2 in N_2 . The cuvette (Parkinson Leaf Chamber, Analytical Development Co.) contained a capacitive humidity sensor and a high-speed fan to increase boundary layer conductance. Boundary layer conductance was estimated for open and rolled leaves using filter paper leaf replicates or calculated from cuvette wind speed and leaf dimensions (NOBEL 1983). Gas-exchange measurements were made at midmorning in the growth chamber; thus, air temperature, relative humidity, and irradiance were as above. Measurements were made at mid-leaf on recently fully expanded leaves held perpendicular to the light source. Net assimilation and stomatal conductance to water vapor (g^{st}) were calculated using the equations of VON CAEMMERER and FARQUHAR (1981) and were based on projected leaf area for both open and rolled leaves. We assumed that cuticular conductance was negligible. To determine the effect of rolling on total leaf conductance, gas-exchange measurements were made while the leaves were rolled and after the leaves were forcibly opened.

Leaf water potential (ψ) was measured on gas-exchange leaves using a Scholander-type pressure chamber (model 1000, PMS Instrument Co., Corvallis, Oreg.). Relative water content (RWC) of midleaf segments was calculated from fresh (FW), saturated (SW), and dry weight (DW) [RWC =

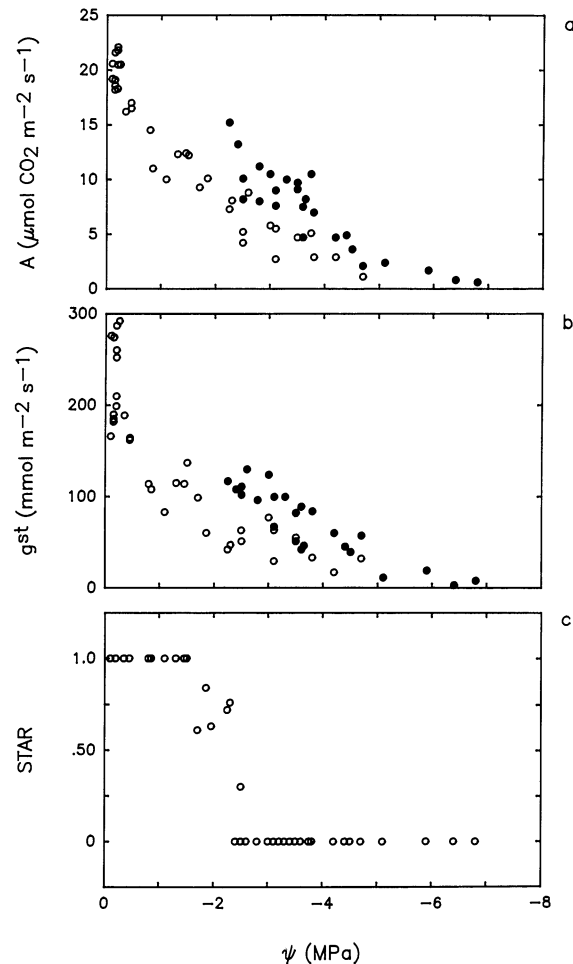


FIG. 2.—Net carbon assimilation (A), stomatal conductance to water vapor (g^{st}), and silhouette-to-total-area ratio (STAR) versus leaf water potential (ψ) of open (\circ) and rolled (\bullet) leaves of *Andropogon gerardii*. After rolling began ($\psi < -1.8$ MPa), data were collected with leaves in a rolled configuration and after forcibly unrolling. See Material and methods for further explanation.

$(\text{FW} - \text{DW})/(\text{SW} - \text{DW})$]. Saturated weight was determined after leaves rehydrated overnight; dry weight was determined after drying at 60 C for 48 h.

The degree of leaf rolling was expressed as the ratio of silhouette (projected) leaf area of rolled leaves (midvein oriented downward) to total projected leaf area following unrolling (CARTER and SMITH 1985). Silhouette-to-total-area ratio (STAR) ranged from one for open leaves to zero for folded leaves of *A. gerardii* and approached zero in rolled leaves of *S. pectinata*.

Energy budget calculations were used to estimate the effect of leaf rolling on E and leaf temperature (T_l). Boundary layer (g^{bl}) and total leaf (g^{tot}) conductance, leaf-to-air vapor pressure deficit (LAVPD), and E were calculated for open leaves of each species using typical values of g^{st} for water-stressed plants (see figs. 2 and 3, open symbols at -3 MPa), and field measurements of

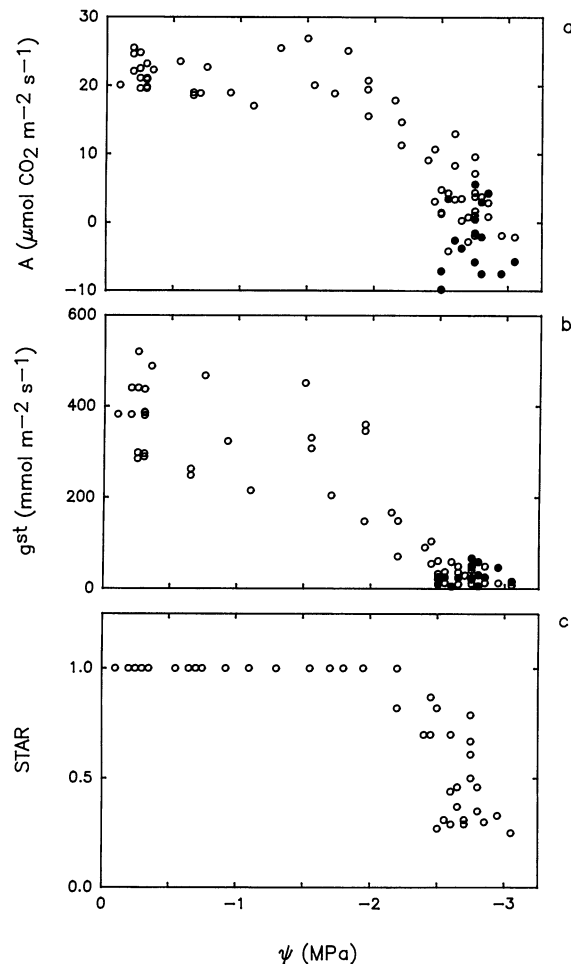


FIG. 3.—Net carbon assimilation (A), stomatal conductance to water vapor (g^{st}), and silhouette-to-total-area ratio (STAR) versus leaf water potential (ψ) of open (\circ) and rolled (\bullet) leaves of *Spartina pectinata*. After rolling began ($\psi < -2.0$ MPa), data were collected with leaves in a rolled configuration and after forcibly unrolling. See Material and methods for further explanation.

air temperature (T_A), T_L , relative humidity, and wind speed (OLD 1969; KNAPP 1984). The above parameters were then calculated for leaves as though they were rolled, incorporating expected changes in boundary layer thickness and incident solar irradiation (S) associated with rolling. Since adaxial stomata of both species were closed in completely rolled leaves, changes in g^{tot} with rolling were attributable to differences in g^{bl} ; g^{st} did not change. Transpiration and g^{st} were expressed as a function of projected area of open leaves (one-half total leaf area), whether leaves were open or rolled, in all energy budget calculations.

Prior to rolling, leaves of *A. gerardii* and *S. pectinata* were strongly arched, but midleaf sections used for gas-exchange measurements were approximately horizontal. Therefore, for energy budget calculations we assumed that open leaves of both species received full sunlight. Because lamina of folded leaves of *A. gerardii* are typically

oriented normal to the sun (personal observation), incident irradiation per unit leaf area (solar and IR) is identical for open and rolled leaves (W. K. SMITH, personal communication). Rolled leaves of *S. pectinata* are essentially cylindrical, so incident solar irradiance must be corrected for cosine effects (i.e., energy flux density on curved surfaces is less than for flat surfaces of equal width because incident irradiation is distributed over more surface area). Cosine corrections were accomplished by multiplying incident solar irradiance by the STAR value of the rolled leaf (W. K. SMITH, personal communication). Absorbed infrared irradiation (from surroundings and sky) does not require cosine correction.

It was assumed that leaf absorptance, reflectance, and angle did not change with rolling. Specific values used in the energy budget calculations were as follows: relative humidity = 40%; barometric pressure = 1,000 mbar; leaf width = 1.0 and 0.5 cm for open and rolled leaves of *A. gerardii*, respectively, and 1.5 and 0.5 cm (STAR = $\frac{1}{3}$) for open and rolled leaves of *S. pectinata*, respectively; wind speed = 1 m s^{-1} ; leaf absorptance of solar irradiation = 0.5 (for both leaf surfaces); reflectance of solar irradiation by surroundings = 0.2; and leaf emittance of infrared radiation = 0.96. Absorptance, reflectance, and emittance coefficients are taken from NOBEL (1983).

Results

The ratio of adaxial to abaxial g^{st} (ad/ab; % of total) was determined for both species in a preliminary experiment. Stomatal conductance in *Andropogon gerardii* was predominantly abaxial (25/75) and was entirely adaxial in *Spartina pectinata* (100/0). Rolled leaves of both species were functionally amphistomatal (i.e., total conductance was identical for top and bottom) because the outer surface of rolled leaves was derived from the abaxial surface of open leaves. Therefore, rolled leaves were treated as having an adaxial to abaxial conductance ratio of 50/50. For completely rolled leaves of *S. pectinata*, adaxial and abaxial conductances were primarily cuticular.

Failure to correct g^{bl} for stomatal distribution can lead to significant errors in calculation of g^{st} . This is especially true when the boundary layer is large, as was the case with the cuvette used in this study. Stomatal and boundary layer conductances are given in table 1 for open well-watered and rolled drought-stressed leaves with either symmetrical (50/50) or asymmetrical (25/75 for *A. gerardii* and 100/0 for *S. pectinata*) distribution of g^{st} . The error in calculation of g^{st} is small (<5%) for both species at low ψ , when leaves are rolled and g^{st} is low. At high ψ when leaves are open and g^{st} is high, however, incorrect assumption of stomatal distribution results in a signifi-

TABLE 1

STOMATAL AND BOUNDARY LAYER CONDUCTANCE OF OPEN WELL-WATERED AND ROLLED DROUGHT-STRESSED LEAVES

	<i>Andropogon gerardii</i>		<i>Spartina pectinata</i>	
	Open	Rolled	Open	Rolled
g^{bl} :				
50/50	1,100	1,350 ^a	1,000	1,070 ^a
25/75, 100/0 ..	825 ^a	1,013	500 ^a	535
g^{st} :				
50/50	224	50 ^a	286	30 ^a
25/75, 100/0 ..	240 ^a	51	400 ^a	31

NOTE.—Units are $\text{mmol m}^{-2} \text{s}^{-1}$ for both stomatal (g^{st}) and boundary layer (g^{bl}) conductance to water vapor. Leaves were treated as having either symmetrical (50/50) or asymmetrical (25/75 and 100/0 for *A. gerardii* and *S. pectinata*, respectively) distribution of g^{st} ; comparisons should therefore be made within columns.

^a Calculations made with the actual distribution of g^{st} for each species and leaf configuration. See Results for further explanation.

cant error in g^{st} (7% in *A. gerardii* and 29% in *S. pectinata*). These errors become very large for *S. pectinata*, which has high maximal g^{st} and a highly asymmetrical distribution of g^{st} . Subsequent gas-exchange data presented in this paper are based on g^{st} distributions of 25/75 and 100/0 for open leaves of *A. gerardii* and *S. pectinata*, respectively, and 50/50 for rolled leaves.

Net carbon assimilation and g^{st} declined continuously with decreasing ψ in *A. gerardii* (figs. 2a and 2b) and ceased at ψ s well below those at which rolling occurred (fig. 2c). Leaf rolling began at ca. -1.8 MPa and was complete by -2.8 MPa. Stomatal closure and hence *A* did not approach zero until ψ s below -6 MPa; therefore, carbon fixation occurred over a wide range of ψ s in rolled leaves of *A. gerardii*. Values of *A* and g^{st} for folded

leaves were ca. twofold higher than values for forcibly opened leaves over the entire range of ψ s when such measurements were made. Thus, adaxial stomata in rolled leaves of *A. gerardii* were closed, and doubling of gas-exchange values with rolling resulted from using half as much leaf area in the calculations. In contrast, *A* and g^{st} in *S. pectinata* approached zero with the completion of leaf rolling (ca. -3 MPa) and remained near zero when these leaves were forcibly unrolled (fig. 3). Leaf rolling is therefore accompanied by cessation of gas exchange in *S. pectinata*.

Leaves were completely rolled by 85% RWC in *S. pectinata* but not until 70% in *A. gerardii*. Net assimilation and g^{st} declined to zero by ca. 85% and 35% RWC in *S. pectinata* and *A. gerardii*, respectively (data not shown).

Our energy budget model predicted decreases in *E* and T_L of 7% and 1.1 C, respectively, in *A. gerardii*, and 13% and 2.0 C, respectively, in *S. pectinata* with rolling (table 2). Decreases in *E* were attributable to reduced LAVPD. The effect of higher g^{bl} associated with rolling on g^{tot} was minor because g^{st} was very small relative to g^{bl} by the time leaf rolling occurred. Reductions in T_L , and thus LAVPD, resulted primarily from increases in sensible (convective and conductive; J^c) heat loss associated with increased g^{bl} following rolling in *A. gerardii* and from reduced *S* in *S. pectinata*.

Discussion

It is often suggested that leaf rolling is important in decreasing *E* under conditions of limited water availability (e.g., OPPENHEIMER 1960; O'TOOLE and CRUZ 1979; BEGG 1980). The contribution of rolling to reducing *E*, however, depends on several factors including stomatal distribution and the degree and pattern of stomatal

TABLE 2

ENERGY BUDGET PREDICTIONS OF THE EFFECT OF LEAF ROLLING ON CONDUCTANCE, TRANSPIRATION, SOLAR IRRADIANCE, SENSIBLE HEAT LOSS, AND LEAF TEMPERATURE

	<i>Andropogon gerardii</i>		<i>Spartina pectinata</i>	
	Open	Rolled	Open	Rolled
g^{bl} ($\text{mmol m}^{-2} \text{s}^{-1}$)	2,067	3,898	1,125	2,688
g^{st} ($\text{mmol m}^{-2} \text{s}^{-1}$)	50	50	30	30
g^{tot} ($\text{mmol m}^{-2} \text{s}^{-1}$)	48.8	49.4	29.2	29.7
LAVPD (mole fraction) ..	.047	.043	.051	.044
<i>E</i> ($\text{mmol m}^{-2} \text{s}^{-1}$)	2.31	2.14	1.50	1.30
<i>S</i> (W m^{-2})	925	925	925	308
J^c (W m^{-2})	534	548	545	211
T_A (C)	35.0	35.0	35.0	35.0
T_L (C)	39.0	37.9	40.0	38.0

NOTE.—Abbreviations are as follows: g^{bl} = boundary layer, g^{st} = stomatal and g^{tot} = total leaf conductance to water vapor; LAVPD = leaf-to-air vapor pressure deficit; *E* = transpiration; *S* = incident solar irradiance; J^c = sensible (convective and conductive) heat loss; T_A = air temperature; and T_L = leaf temperature. See Material and methods for further explanation.

opening at low ψ . For example, adaxial stomata are closed in rolled leaves of *Andropogon gerardii* and *Spartina pectinata* (this study), but remain partially opened in rolled leaves of rice (O'TOOLE and CRUZ 1980). O'TOOLE and CRUZ (1979) observed significant decreases in E when well-watered leaves of rice were artificially rolled. However, leaf rolling is normally accompanied by decreases in ψ and g^{st} ; thus their study overestimates the contribution of rolling to reduced E . No one has determined the effect of rolling on E in water-stressed plants by measuring E of rolled and forcibly opened leaves. Our calculations suggest that for water-stressed *A. gerardii* and *S. pectinata*, E is indeed lower in rolled relative to opened leaves. However, the magnitude of this decrease is small.

To estimate the contribution of leaf rolling to water conservation beyond that associated with stomatal closure, we calculated the percentage reduction in E attributable to rolling versus reduced g^{st} . Transpiration rates were calculated for typical well-watered leaves ($g^{st} = 240$ and 400 $\text{mmol m}^{-2}\text{s}^{-1}$ for *A. gerardii* and *S. pectinata*, respectively) using the same climatic data used in the energy budget calculations, except that leaf temperatures were assumed to be 2 C lower than those given for open leaves in table 2 because of increased latent (evaporative) heat loss. These values were compared to E of rolled and opened water-stressed leaves (table 2). Stomatal closure alone caused a decrease in E of 73% for *A. gerardii* and 88% for *S. pectinata*. Leaf rolling decreased E an additional 2% in each species. Thus, leaf rolling was of secondary importance in reducing water loss relative to stomatal closure for these species.

O'TOOLE and CRUZ (1980) and REDMANN (1985) suggested that partial leaf rolling may serve to increase g^{st} by providing a more favorable microenvironment, such as increased relative humidity, for adaxial stomata. In rice, adaxial g^{st} was less sensitive to water stress than was abaxial g^{st} (O'TOOLE and CRUZ 1980). We saw no evidence of a differential response of adaxial versus abaxial stomata to drought for *A. gerardii*. In a preliminary experiment, the ratio of adaxial to abaxial g^{st} remained unchanged prior to completion of leaf rolling (unpublished data). If g^{st} were enhanced, the repercussions for whole plant water loss would probably be minimal, given the narrow range of ψ s over which rolling occurs in most species. Leaves are likely to be either completely open or rolled.

Leaf rolling augments stomatal closure by increasing leaf resistance to water loss (JOHNS 1978; O'TOOLE and CRUZ 1979). Overlapping leaf surfaces increase effective cuticular resistance for enclosed portions of the leaf. While this serves to reduce water loss, in most species it also severely

restricts potential carbon gain and may put the plant at a competitive disadvantage. Leaf rolling coupled to complete stomatal (en)closure is consistent with a drought avoidance strategy and might be expected in mesic species. Leaf rolling and stomatal closure are complete by -3 MPa in *S. pectinata*. *Andropogon gerardii*, in contrast, maintains positive A and g^{st} at ψ s below -6 MPa (this study; KNAPP 1985), well after rolling occurs. Because leaves of *A. gerardii* fold rather than roll, resistance to water loss and hence carbon gain is not as great in closed leaves. The leaf rolling strategy of *A. gerardii* is therefore consistent with its relatively high degree of drought tolerance.

The narrow range of ψ s over which leaf rolling occurs in *A. gerardii* and *S. pectinata* is similar to other species (*Sorghum bicolor* [BEGG 1980]; *Oryza sativa* [O'TOOLE and CRUZ 1980]; *Agropyron dasystachyum* [RIPLEY and REDMANN 1976]). This range is shifted to lower ψ s in field-grown plants, plants grown in larger pots, and plants that have experienced successive droughts (personal observation). Thus, the level of water stress at which rolling occurs appears to depend on growth conditions and drought preconditioning.

Energy budget calculations indicated that leaf rolling in *A. gerardii* and *S. pectinata* decreases T_L and E by increasing J^c and reducing S . Because of decreases in T_L , rolling probably also increases A and water-use efficiency. The photosynthetic temperature optimum for *A. gerardii* is ca. 30–34 C (KNAPP 1985), and T_L is likely to be higher than this during drought (KNAPP 1984). Increases in leaf angle and reflectivity were not considered in this study but accompany rolling in many species and would further reduce T_L and E (RIPLEY and REDMANN 1976; BEGG 1980). Additionally, in the hot, sunny, and dry environment of the tallgrass prairie, leaf rolling, through reduced irradiance and T_L , may serve to decrease the probability of photoinhibition. GAMON and PEARCY (1989) observed photoinhibitory damage in *Vitus californica* when paraheliotropic leaf movement was restricted. Similarly, curling reduced photoinhibitory damage in desiccated *Selaginella lepidophylla* (LEBKUECHER and EICKMEIER 1990). Decreases in E and T_L associated with rolling, though small, may increase the probability of survival of grasses in water-limited prairie habitats.

Acknowledgments

We thank W. K. SMITH for his assistance with the energy budget calculations and A. K. KNAPP for providing seeds. We also thank the anonymous reviewers whose input greatly improved this paper. This research was supported in part by grants from USDA CRGO (Forest Biology and Stratospheric Ozone Depletion Programs) to EVAN H. DeLUCIA.

LITERATURE CITED

- BARNES, P. W. 1985. Adaptation to water stress in the big bluestem-sand bluestem complex. *Ecology* **66**:1908-1920.
- BEGG, J. E. 1980. Morphological adaptations of leaves to water stress. Pages 33-42 in N. C. TURNER and P. J. KRAMER, eds. *Adaptation of plants to water and high temperature stresses*. Wiley, New York.
- BROWN, L. F., and M. J. TRILICA. 1977. Interacting effects of soil water, temperature, and irradiance on CO₂ exchange rates of two dominant grasses of the shortgrass prairie. *J. Appl. Ecol.* **14**:197-204.
- CARTER, G. A., and W. K. SMITH. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiol.* **79**:1038-1042.
- EHLERINGER, J., and I. FORSETH. 1980. Solar tracking by plants. *Science* **210**:1094-1098.
- EPSTEIN, E. 1972. *Mineral nutrition of plants: principles and perspectives*. Wiley, New York.
- FORSETH, I. N., and J. R. EHLERINGER. 1983. Ecophysiology of two solar tracking desert winter annuals. IV. Effects of leaf orientation on calculated daily carbon gain and water use efficiency. *Oecologia* **58**:10-18.
- GAMON, J. A., and R. W. PEARCY. 1989. Leaf movement, stress avoidance and photosynthesis in *Vitis californica*. *Oecologia* **79**:475-481.
- JOHNS, G. G. 1978. Transpirational, leaf area, stomatal and photosynthetic responses to gradually induced water stress in four temperate herbage species. *Aust. J. Plant Physiol.* **5**:113-125.
- KEMP, P. R., and G. J. WILLIAMS III. 1980. A physiological basis for niche separation between *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄). *Ecology* **61**:846-858.
- KNAPP, A. K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *Am. J. Bot.* **71**:220-227.
- . 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* **66**:1309-1320.
- KNAPP, A. K., and F. S. GILLIAM. 1985. Response of *Andropogon gerardii* (Poaceae) to fire-induced high vs. low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. *Am. J. Bot.* **72**:1668-1671.
- LEBKUECHER, J. G., and W. G. EICKMEIER. 1990. Desiccation-induced plant curling and high-irradiance damage in the desert resurrection plant *Selaginella lepidophylla*. *Bull. Ecol. Soc. Am.* **71**:227.
- NOBEL, P. S. 1983. *Biophysical plant physiology and ecology*. Freeman, New York.
- OLD, S. M. 1969. Microclimate, fire, and plant production in an Illinois prairie. *Ecol. Monogr.* **39**:355-384.
- OPPENHEIMER, H. R. 1960. Adaptation to drought: xerophytism. Pages 105-138 in *Plant-water relationships in arid and semi-arid conditions: reviews of research*. Unesco, Paris.
- O'TOOLE, J. C., and R. T. CRUZ. 1979. Leaf rolling and transpiration. *Plant Sci. Lett.* **16**:111-114.
- . 1980. Response of leaf water potential, stomatal resistance, and leaf rolling to water stress. *Plant Physiol.* **65**:428-432.
- REDMANN, R. E. 1971. Carbon dioxide exchange by native Great Plains grasses. *Can. J. Bot.* **49**:1341-1345.
- . 1985. Adaptation of grasses to water stress: leaf rolling and stomate distribution. *Ann. Mo. Bot. Gard.* **72**:833-842.
- RIPLEY, E. A., and R. E. REDMANN. 1976. Grassland. Pages 349-398 in J. L. MONTEITH, ed. *Vegetation and the atmosphere*. Vol. 2. Case studies. Academic Press, London.
- VON CAEMMERER, S., and G. D. FARQUHAR. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**:376-387.
- WEAVER, J. E., and T. J. FITZPATRICK. 1932. Ecology and relative importance of the dominants of tall-grass prairie. *BOT. GAZ.* **93**:113-150.